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Systematic status of the Black-collared Bulbul *Neolestes torquatus*

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The Afrotropical monotypic genus *Neolestes* has been treated variously as a bulbul (Pycnonotidae) or a 'shrike' (Malaconotidae, Laniidae or Prionopidae). Recent field observations and fresh laboratory material have enabled a multi-disciplinary review incorporating biology, anatomy and DNA. The DNA analysis suggests that *N. torquatus* represents a deep branch of the pycnonotid clade. The plumage of *Neolestes* is unlike that of any bulbul, although the juvenile plumage is more bulbul-like than shrike-like. Evidence from the syrinx, skull, humerus and carpometatarsus eliminates a relationship between *Neolestes* and the shrikes and mainly points to one with the Pycnonotidae. *Neolestes* could be the primitive sister-group of the Pycnonotidae, or a member of some larger group of which the bulbuls are but one manifestation. The vocalizations are not shrike-like but are reminiscent of those of the African species of *Pycnonotus*; other aspects of its behaviour point in this direction. We believe there is no evidence for considering *Neolestes* to be a 'shrike', and recommend treating it as a primitive member of the Pycnonotidae, although as *incertae sedis*.

The Black-collared Bulbul *Neolestes torquatus* was described by Cabanis (1875) as a monotypic species in a monotypic genus. He found it difficult to identify the nearest relatives of *Neolestes*, which he treated tentatively as an aberrant member of the Malaconotinae. Gadow (1883) followed suit in placing *Neolestes* as an unnumbered genus, at the end of the Malaconotinae, but with a footnote (p. 103) stating that it 'does not appear to be a Bush-Shrike, but to be allied to the Bulbuls or Pycnonotidae', a conclusion based mainly on bill morphology. Unfortunately the association of *Neolestes* with the Malaconotinae in Gadow's influential catalogue seems to have carried more weight than his parenthetical opinion, which has almost always been overlooked.

Shelley (1896), presumably swayed by the undeniable similarities in plumage pattern, went so far as to include *Neolestes* in the now-abandoned genus *Pelicinius*, which in his treatment included species that are all now referred to the bush-shrike genus *Telophorus* (type-species the Bokmakierie *T. zeylonus*), which is now often included in *Malaconotus* (type-species Grey-headed Bush Shrike *M. blanchoti*). (*Pelicinius* is now considered a synonym of *Laniarius*). In his continuation of Shelley's work, Sclater (1912) placed *Neolestes* in the 'Laniariinae', between *Telophorus* and *Malaconotus*.

The most influential appraisal of the relationships of *Neolestes* was that of Chapin (1921), who presented evidence suggesting that it was in fact an aberrant bulbul (Pycnonotidae). He knew the species well in the field; his later experience did not change his view (Chapin 1953) but rather prompted him to rule out completely any idea of a relationship with the Malaconotinae. This was perhaps rather precipitate, but has been the practice followed by most subsequent writers. Sclater (1930) put *Neolestes* in an enlarged Laniidae, between *Nicator* and *Lanioturdus*, but he gave it the English name 'Black-collared Bulbul' and mentioned the views of Chapin (1921) in a footnote. Bannerman (1936) omitted *Neolestes* in his treatment of the Pycnonotidae and thus had to include it with the

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Laniidae in a later volume, apologetically citing Chapin in a footnote (Bannerman 1939). Bannerman also covered all fronts by giving it the English name 'Black-collared Bulbul-Shrike'! Delacour (1943) questioned the pycnonotid affinities of *Neolestes*, while believing it not to be a shrike. Apart from the fact that Bannerman (1953) did not trouble to make any changes to his earlier account when he published his condensed handbook, in the literature *Neolestes* has remained a bulbul ever since, based mainly on the authoritative position taken by Chapin (1953).

Thus practically throughout its history, the question has been: 'Is *Neolestes* a bush-shrike (Malaconotinae) or a bulbul (Pycnonotidae)?' More recently, Olson (1990) examined a fluid-preserved specimen and tentatively suggested placing *Neolestes* as *incertae sedis*, nearest to the helmet-shrikes (Prionopidae). Although Keith *et al.* (1992) illustrated this species with the Pycnonotidae, they accepted the proposal of Olson and intend treating *Neolestes* with the shrikes, in a later volume. Sibley and Monroe (1990) and Dowsett and ForbesWatson (1993), however, provisionally retained *Neolestes* with the Pycnonotidae, although as *incertae sedis*.

Neolestes torquatus is a species of lightly wooded savannas, occurring in a belt across central Africa, mainly south of the equator. It is confined to Angola, Congo, Gabon (of very local distribution), Zaire and the extreme northwest of Zambia, a distribution that agrees well with the Guineo–Congolian/Zambezian transition zone of White (1983). The extreme limits of its range are from Lubango (ex-Sa da Bandeira) in Angola, where it is evidently rare (W.R.J. Dean, pers. comm.), northwards to Tchibanga in Gabon (Malbrant & Maclatchy 1949) and further north to the Odzala area in Congo (Dowsett-Lemaire 1997). Eastwards it occurs to extreme eastern Zaire on Idjwi Island, Lake Kivu (Prigogine 1967). It ranges southward throughout the savannas of Zaire to the Marungu highlands (Dowsett & Prigogine 1974). In Zambia, it occurs no farther south than Mwinilunga district (Benson *et al.* 1971). *Neolestes* is common from about sea-level to 1750 m, and occurs in small numbers as high as 2060 m in the Marungu area (Dowsett & Prigogine 1974).

METHODS

Olson (1990) stressed that more satisfactory skeletal material was needed for a thorough study; with this aim R.J.D. and F.D-L. collected a specimen in the Odzala area of northern Congo (00°36′N,14°54′E). As well as making available to S.L.O. the whole body preserved in spirit, they also collected tissues for DNA analysis by M.S.R.

Field studies

R.J.D. and F.D-L. (either singly or together) have studied *Neolestes* in Congo, Zaire and Zambia; R.J.D. has handled live examples captured in mist-nets in all three areas. Tape recordings were made by F.D-L. and copies are available through C. Chappuis (France) and the National Sound Archives (London).

Anatomical studies

The specimen was preserved whole in ethanol after examination in the field, with the exception of some organs which were extracted for separate DNA analysis. Upon dissection, S.L.O. preserved the skin in fluid, as well as the tongue, trachea and syrinx, while the skeleton was prepared by using trypsin.

S.L.O. studied the syrinx, carpometacarpus, nasal ossification and the structure of the skull and humerus, comparing these (together with study skins) directly to specimens in the National Museum of Natural History, Smithsonian Institution, Washington DC, where the specimen is preserved as USNM 620817.

DNA analysis

M.S.R. undertook the analyses at the Department of Population Biology, University of Copenhagen. For the analysis, 282 bp of cytochrome *b* sequence were compared between *Neolestes torquatus* and the following members of several passerine families: Pycnonotidae (Eastern Mountain Greenbul *Andropadus nigriceps*, Yellow-streaked Bulbul *Phyllastrephus flavostriatus* and Western Nicator *Nicator chloris*), Sylviidae (Green Warbler *Phylloscopus nitidus*, genbank accession number 773489, Helbig *et al.* 1995), Paridae (Great Tit *Parus major*, genbank accession number D38314, K. Chikuni, N. Minaka & H. Ikenaga unpubl. data, and Plain Titmouse *Parus inornatus*, genbank accession number X60944, Edwards *et al.* 1991), Prionopidae (White Helmet Shrike *Prionops plumatus*) and Malaconotidae (Bulo Burti Boubou *Laniarius liberatus*, Smith *et al.* 1991), Corvidae (Jungle Crow *Corvus macrorhynchus*, genbank accession number D38313, K. Chikuni *et al.* unpublished, and Blue Jay *Cyanocitta cristata*, genbank accession number X74258, Cracraft 1993) and Turdidae (Eye-browed Thrush *Turdus obscurus*, genbank accession number D38323, K. Chikuni *et al.*

unpubl. data). The South American suboscine Baron's Spinetail *Cranioleuca baroni* was used as an outgroup (J. Garcia-Moreno unpubl. data).

Blood or tissue samples of *A. nigriceps, P. flavostriatus, P. plumatus, N. chloris* and *N. torquatus* were washed three times in blood buffer (50 mM Tris pH 7.5, 400 mM NaCl, 100 mM EDTA, 0.5% SDS) and subjected to standard proteinase K, phenol/chloroform extractions (Arctander 1988). The primer pair L14841 and H15149 (Kocher *et al.* 1989) was used to amplify and sequence 282 base pairs of the cytochrome *b* gene. Sequencing of both strands was accomplished by initially amplifying the target sequence with one of the primer pair biotinylated. Dynabeads (DynalR) were used to separate the strands of the amplified product and dideoxy sequencing was carried out as normal using the non-biotinylated primer.

Sequences were aligned visually using the program SeqApp (Gilbert 1992). Aligned sequences were analysed using PAUP (version 3.1 Swofford 1991) in order to infer phylogenetic relationships; CS3 (Siegismund unpubl. program) was used to compare substitution patterns.

We follow Dowsett and Forbes-Watson (1993) in recognizing the Pycnonotidae (bulbuls), Malaconotidae (bush-shrikes), Laniidae (true shrikes) and Prionopidae (helmet shrikes) as separate families. For the sake of discussion at the generic level, it is more convenient here to consider *Telophorus* as a genus apart from *Malaconotus* (following Olson 1990).

RESULTS AND DISCUSSION

Field studies

The nest and eggs have been well described (Chapin 1953 p.156, Bowen 1983). They are similar to those of savanna Pycnonotidae in all respects, with the nest being a frail cup of slender grass and plant stems and the eggs oval, coloured pinkish white with darker pink and rufous speckles and shading. However, the nests and eggs of true shrikes (Laniidae) and bush-shrikes (Malaconotidae) are also similar to this. Lippens and Wille (1976) considered the eggs to be very different from those of other bulbuls, but did not explain this and a comparative study would be needed to confirm it.

There are at least four nests for which contents were known with certainty; three of these contained two eggs, the other contained two chicks (Bowen 1983, Chapin 1953, Lippens & Wille 1976, Salvan 1972). The most common clutch size in Pycnonotidae and Malaconotidae in central and southern Africa is two eggs; four is exceptional (R.J. Dowsett & J.F.R. Colebrook-Robjent, unpubl. data). In the Laniidae, however, four eggs are more common, while in Prionopidae a clutch of four is the commonest, with groups of these co-operatively breeding birds laying up to seven eggs in one nest. In contrast to the large parties formed by helmet-shrikes, *Neolestes* has never been reported in any more than small groups of up to four birds (presumably family groups). In this respect the evidence from *Neolestes* points to it possibly belonging to the Pycnonotidae and almost certainly not to the Prionopidae. The young are born naked (Bowen 1983), which is a character shared by all Pycnonotidae and at least some Malaconotidae, while the evidence in Prionopidae is unclear (Markus 1972).

The species has a mixed fruit–insect diet (various observers), the strong fruit element being typical of bulbuls and rare or unknown in most Laniidae and Malaconotidae. A nestling was almost invariably fed fruit, both adults sharing this duty (Bowen 1983).

For a discreet species usually feeding low in dense herbaceous vegetation, the song is the best way of locating the bird, as it is given from the top of a bush or small tree (F.D-L.). In northern Congo, song was heard throughout the year, with some seasonal fluctuations. Both songs and call-notes are reminiscent of those of the African species of *Pycnonotus*, especially the Common Bulbul *P. barbatus*; they are quite unlike the vocalization of any shrike.

Plumage

Neolestes torquatus is a distinctively and boldly patterned bird with whitish underparts, a broad iridescent blue-black band across the breast that is continuous with a stripe of similar colour extending through the eye and over the auriculars to the neck. The crown and nape are grey; the back, wings and tail are green; and the underwing coverts and bend of the wings are bright yellow.

Various combinations of such plumage can be found elsewhere with the *Telophorus* and *Malaconotus* bush-shrikes, although the whitish underparts are unusual, occurring only in *T. bocagei*. This colour pattern is what led to the former placement of *Neolestes* with the shrike-like birds.

Another curious feature is the tuft of stiff, plush, chestnut feathers behind the ear, which Olson (1990) noted was similar to the dark tuft of feathers in helmet-shrikes of the genus *Prionops sensu stricto* (although, as noted below, S.L.O. is now convinced that the differences in cranial osteology rule out any relationship between *Neolestes* and *Prionops*).

Chapin (1921) remarked that the black eyestripe passes over the ear-coverts in *Neolestes* but under them in those shrikes that have such markings, whereas in fact in several species of the latter the stripe may pass *through* the auriculars. Chapin (1921) thought that there was only a 'superficial resemblance' between *Neolestes* and bush-shrikes, and later he went further (Chapin 1953) in saying that it 'has no real resemblance to a shrike'. What he failed to stress is that *Neolestes* certainly bears no resemblance whatsoever to any bulbul in plumage pattern. No bulbul has so much as a black breast band, the closest approach being the blackish pectoral patches in the Red-whiskered Bulbul *Pycnonotus jocosus*, which nearly reach across the breast. Given that there is nothing in the plumage pattern alone to suggest a relationship of *Neolestes* with anything other than the Malaconotidae, it is little wonder that early museum taxonomists placed the genus among the shrikes.

Filoplumes

One of the characters long associated with the Pycnonotidae by skin-taxonomists is the presence of well-developed filoplumes on the nape. This condition, as determined by Olson from examination of the Smithsonian collections, is indeed widely distributed in the species attributed to this family. Filoplumes are present in some species in virtually every genus, with exceptions including genera of doubtful affinity such as *Nicator*. Nevertheless, elongate filoplumes in the nape could not be found in certain species that otherwise seem certainly to be correctly identified as bulbuls. Not only is this character thus not invariably present; it also occurs in other families. The fact that *Neolestes* lacks such filoplumes, as also noted by Chapin (1921), seems to have little taxonomic significance.

The juvenile plumage (Chapin 1953, pers. obs.) is like a duller version of that of the adult; but the crown and nape are greenish (like the upper back), not grey as in adults – and not brownish, as illustrated by Keith *et al.* (1992). The black breast band develops early in the juvenile, but is dull, not glossy. The juvenile wing differs in the buffy tips to some of the greater coverts. As mentioned by Chapin, there is no sign of the fine barring present in the first plumage of Laniidae *sensu lato*. The specimen collected was a juvenile as shown by the pale buff tips remaining on some wing coverts and by the small fleshy rictal flanges. The skull was nevertheless well ossified, although the parietals were largely unpneumatized (untrabeculated).

In contrast to such genera of Pycnonotidae as *Phyllastrephus* and *Bleda*, there is no sexual dimorphism in size (but neither is there in such genera as *Pycnonotus*). Bowen (1983) summarizes wing lengths of sexed specimens: male 67–76 mm (mean 72.9 mm, $n = 17$), female 68–76 mm (mean 72.7 mm, $n = 12$).

Morphology

Syrinx

The syrinx in *Neolestes* was similar to that examined in a specimen of the Sombre Bulbul *Andropadus importunus*, but markedly different from the syrinx in the Helmet Shrike *Prionops plumatus* (Olson 1990) or of the Bush Shrike *T. zeylonus* (examined in this study). That of *P. plumatus* is unusual in that the ventral musculature is broad and elongate, and is asymmetrical, with fibres from the left side crossing the midline to the right side of the trachea, which is possibly twisted. The syrinx in one individual of *T. zeylonus* was similar to that of *Prionops* in having the elongate ventral musculature, but was not asymmetrical.

Syringeal morphology of bulbuls, shrikes and possible allies has not been subjected to detailed study, in contrast, for example, with thrushes and their possible relatives (Ames 1975). However, it would seem that theirs is otherwise a very generalized syringeal morphology that is probably similar to that in a great many oscines. Although the syrinx neither confirms nor refutes a pycnonotid relationship for *Neolestes*, it does appear to rule out any affinity with *Prionops* or the Malaconotidae.

Carpometacarpus

In *Neolestes* there is a distinct, reasonably well-developed dentiform process ('process D'; Pocock 1966) on the leading edge of the major metacarpal above the tendinal groove, curving over this last. This character is present in many oscines. In Pocock's (1966) initial study examining the taxonomic utility of this character, he noted that the process was absent in the Laniidae *sensu lato* (including Malaconotidae), but present or weakly developed in the Pycnonotidae. This was confirmed by P.L. Ames (pers. comm.) who found the process to be absent in 29 species in 11 genera of Laniidae *sensu lato*, but variable at the generic and specific level in the Pycnonotidae.

Because the process occurs in many other families of birds, its presence in *Neolestes* cannot be taken by itself to imply relationships with the Pycnonotidae, but it strongly suggests that the genus does not belong among the shrikes.

Nasal ossification

Examination of a fluid-preserved specimen of *Neolestes* had shown no ossification of the nostril; however, that examination was regarded as inconclusive without a proper skeletal preparation (Olson 1990). In the present specimen of *Neolestes*, it can be confirmed that the posterior margin of the bony nostril was entire, with no trace of pycnonotid-like ossification of the posterior margin.

One of the best characters defining the Pycnonotidae is this ossification of the margin of the nostril, which is present in every genus of the family except a few whose relationships had been questioned (Olson 1990). This ossification may range from the most advanced state, in which there is a distinct sheet of bone covering the posterior third or more of the nostril that is perforated by neural or nutrient foramina, to a few ragged bony outgrowths along the margin of the nostril, the rest of the sheet presumably being cartilaginous.

Thus, what would be the most satisfactory evidence for a pycnonotid relationship of *Neolestes* is lacking in the genus. This is not necessarily proof that *Neolestes* is not a bulbul. S.L.O. has examined all available skeletons of African Pycnonotidae in the USNM collections.

All of the genera are represented and all of the available species of these genera have the nasal ossification, except for *Nicator* (Olson 1990) and for some individuals of the genus *Andropadus* (which are often included in *Pycnonotus*). The nostril was strongly ossified in all 11 individuals of Little Greenbul *A. virens* examined and two of Yellow-whiskered Greenbul *A. latirostris*. It was less developed in three Stripe-cheeked Greenbul *A. milanjensis* and two *A. nigriceps*.

In the Cameroon Sombre Greenbul *A. curvirostris*, the condition was well developed in two individuals and absent in three others; in Slender-billed Greenbul *A. gracilirostris* it was slightly developed in one and absent in four; ossification was absent in two specimens each of Little Grey Greenbul *A. gracilis* and *A. importunus*.

Whether the absence of this nasal ossification in these bulbuls is primitive or a secondary loss cannot be ascertained. What is certain, however, is that *Neolestes* also lacks this character, but in plumage it bears no similarity whatever to the 'sombre bulbuls'.

Skull structure

The skull of *Neolestes* was compared particularly with that of *Telophorus* and also *Malaconotus sensu stricto*, among the bush-shrikes. Because Chapin (1921) considered *Neolestes* to be closest to *Pycnonotus* itself, skull comparisons were made with African species of that genus, including *Andropadus*. On this basis, the overall similarities of the skull of *Neolestes* are decidedly with the bulbuls and not with the shrikes.

As might be expected from external morphology, the rostrum of *Neolestes* is not heavy and shrike-like, but it also differs from that of *Pycnonotus* in being shorter, broader and more decurved. As in bulbuls, there is no nasal septum – a character well developed in *Telophorus* but absent in *Malaconotus sensu stricto* The maxillopalatines are long, thin and slightly expanded at the tips, as in bulbuls, and quite unlike the short, wide and heavy processes in shrikes. The palatines are expanded and truncate posteriorly, lacking transpalatine processes, and in lateral view they descend ventrally below the jugal bar, unlike those of shrikes. The transpalatine processes may be present or absent in *Pycnonotus sensu lato* and when absent the palatines are truncate, as in *Neolestes*, though not quite as expanded. In the shrikes, the transpalatine processes are much stronger. The postorbital process is vestigial in *Neolestes* and *Pycnonotus*, and well developed in *Malaconotus*.

Humerus

All the taxa in question here have a single pneumatic tricipital fossa of the humerus. However, in *Neolestes* and *Pycnonotus* there is an incipient accessory fossa partially undercutting the head, whereas this is absent in *Malaconotus*. Several other differences between *Pycnonotus* and the shrikes were noted in the proximal end of the humerus; in all of these *Neolestes* agreed with the bulbuls, although a larger survey will be needed to determine the taxonomic distribution of these characters.

Molecular results

Substitution patterns

Analysing the 12 in-group species across 282 bp of cytochrome *b* revealed 1481 transitions (ts) and 1140 transversions (tv), with an average ts/tv ratio of 1.36. As expected when comparing distant taxa using cytochrome *b*, third codon positions were almost saturated with respect to transitions (average ts/tv ratio = 1.28; Edwards *et al.* 1991). For this reason the phylogenetic analysis disregarded transitions at third positions as well as first position C–T leucine transitions (a frequent silent substitution prone to saturation; P. Arctander pers. comm.).

Phylogenetic inference

Six most parsimonious trees were generated, which differed only in the terminal branching order of the monophyletic clade containing the Laniidae and Corvidae. All trees placed *N. torquatus* as a sister taxon to the Pycnonotidae as represented by *A. nigriceps* and *P. flavostriatus*. This association is also supported when bootstrap resampling analysis is applied. In addition, the Corvidae and Laniidae present a monophyletic clade that is supported over 1000 bootstrap replicates. This analysis also suggests that *Nicator chloris* is not allied to the Malaconotidae as recently suggested (Keith *et al.* 1992). Instead it groups within a monophyletic clade together with *Parus major* and *P. inornatus*, although this association is not supported by bootstrap analysis (Fig. 1). The same overall clade membership is derived when the outgroup is omitted and an unrooted phylogeny constructed (data not shown). Using this regime, higher bootstrap values for major clades including the close association between *N. torquatus* and the pycnonotid clade were produced.

Conclusions

Despite limited data due to the removal of third codon position transitions, the DNA analysis provided good support for the grouping of *N. torquatus* together with other Pycnonotidae in a monophyletic clade. Within this clade, *Neolestes* was found to be basal, although its exact evolutionary position cannot be ascertained until a phylogenetic analysis considers all members of the Pycnonotidae together with additional outgroups.

In its biology, *Neolestes* exhibits an impressive number of differences from the shrikes, and similarities to the Pycnonotidae. Breeding behaviour (clutch-size and the absence of co-operative breeding), diet (frugivory), vocalizations and juvenile plumage all point to it probably being a bulbul and certainly not a shrike.

The only real divergence is in the plumage of *Neolestes*, which is quite unlike that of any bulbul; it most resembles (at least superficially) the pattern seen in some of the malaconotine shrikes. Evidence from the syrinx, skull, humerus and carpometatarsus provide no further support for a relationship of *Neolestes* to the shrikes, however. The same elements show no important points of departure of *Neolestes* from the conditions obtaining in the Pycnonotidae. Many or all of these similarities may, however, simply be those of some primitive group of primarily frugivorous oscines and may well occur in other taxa. *Neolestes* lacks the nasal ossification of most bulbuls, which, had it been present, would have been the most satisfactory evidence of its relationships to the Pycnonotidae. This absence is probably primitive. *Neolestes* could be the primitive sister-group of the Pycnonotidae or a member of some larger group of which the bulbuls are but one manifestation.

We recommend, following Dowsett and Forbes-Watson (1993), the retention of *Neolestes* with the Pycnonotidae, although as *incertae sedis*.

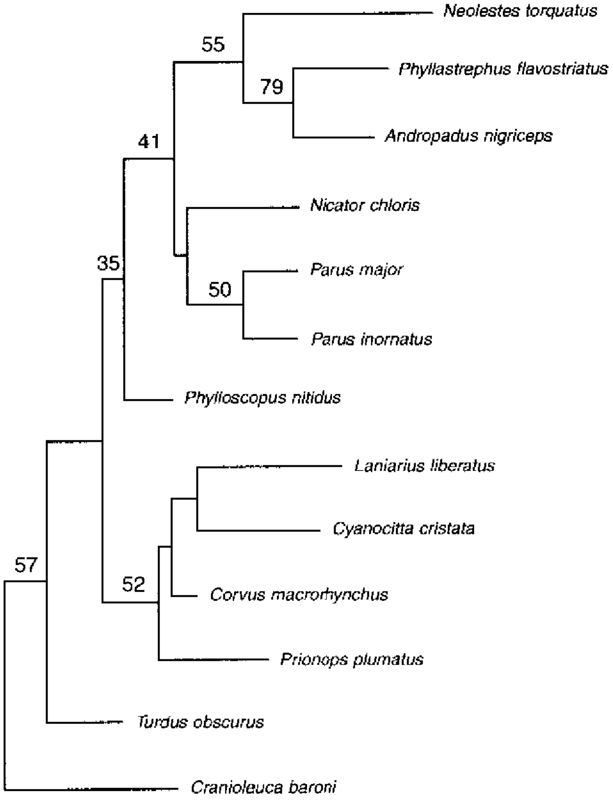

Figure 1. One of six most parsimonious trees (PAUP) generated from the comparison of 282 bp of cytochrome *b* from 13 species of passerines. Other trees differed only in branching order of the terminal nodes of the corvid/laniid clade. This tree has a length of 143 steps and a consistency index excluding uninformative characters of 0.490. Bootstrap percentages over 1000 replicates are indicated above branches.

R.J.D. and F.D-L. undertook their research in Congo while employed by the ECOFAC project (funded by the European Union).

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